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VARIATION IN ASTER ANOMALUS

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Assistant Professor of Botany in the Henry Shaw School of Botany of Washington University

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I. Introduction

Among the higher plants relatively few species have been so intensively studied and described that the interested reader can gain a clear morphological conception of the species as a whole. The dearth of such information would seem to be one of the main reasons why modern biologists have such widely divergent views as to the nature of species. Most of our data on the species problem have been gleaned indirectly from taxonomic work. But taxonomists have been interested mainly not in the nature of species but in the practical classification of the groups with which they were working. Considering the enormous number of groups still awaiting monographic treatment they have probably been wise in applying themselves to the task in hand and eschewing theoretical considerations.

It has, however, seemed to the writer that the nature of species may very properly be taken up as a study in itself, to be investigated for its own sake. It may be that a closer analysis will only reveal the hopeless complexity of the problem and the impossibility of establishing any generalizations. On the other hand, it seems possible that morphological relationships between the individuals which go to make up a species may be uniform enough to yield important generalizations upon further study.

With this end in view, a few relatively simple Linnaean species have been intensively studied as to their morphology, geographical distribution, and the genetic relationships within the species and with other species. The main body of the work has been confined to the genus *Iris*, and it was therefore thought wise to study a few other species from widely separated groups of plants. *Aster anomalus* Engelm. was one of those chosen, for though it belonged to one of the most difficult genera in the Compositae it seemed to be a simple, well-differentiated species. The following data are admittedly meagre in several respects, but no further work is being planned with the species because of inherent technical difficulties in making controlled pollinations, raising large numbers of seedlings, etc. The following brief account does at least present a small body of codified information for one species of the genus *Aster*, a group where such information, though badly needed, is practically non-existent.

ACKNOWLEDGMENTS

For much helpful information on taxonomic points the author is deeply indebted to his colleague, Dr. J. M. Greenman. For the loan of herbarium specimens from the Field Museum and the Gray Herbarium he is greatly obliged to the curators of those institutions. Dr. J. Paul Goode has kindly allowed the use of his copyrighted map in fig. 1.

II. Taxonomy and Morphology

Aster anomalus Engelm. in Torr. & Gray, Fl. N. Am. **2**: 503. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 181. 1884; Gray's Manual, ed. 7, 807. *fig. 936.* 1908; Britton & Brown, Ill. Flora, ed. 2, **3**: 413. *fig. 4296.* 1913; Small, Fl. Southeast. U. S., ed. 2, 1213. 1913.

Slender herbaceous perennials, somewhat pubescent and scabrous, 2-10 dm. high; stems simple or racemosely branched above; young leaves ovate, often deeply serrate, purplish beneath; cauline leaves firm in texture, entire or occasionally subserrate, the lower leaves ovate to ovate-lanceolate, deeply cordate at the base, on slender naked petioles, the upper ones small, subsessile; heads large, hemispherical; involucre several-seriate, bracts acute, appressed at the base, apex strongly reflexed; rays 20–45, bright lavender-blue; achenes brownish, glabrous, ovate-lanceolate, with 3–5 prominent ribs; pappus brownish.

Aster anomalus is marked by its peculiar combination of characters. In common with its closest relatives, *A. azureus* Lindl. and *A. Shortii* Lindl., it has bright blue flowers and cordate lower leaves of firm texture. Unlike them, it has a large number of ray-flowers and strongly reflexed involucral bracts. The resulting combination is unlike any other member of the genus and was well described (Torr. & Gray, Fl. N. Am. **2**: 503. 1843) in a note appended to the original description: "A most remarkable species with nearly the foliage of *Aster Shortii* while the heads and involucre much resemble those of *A. oblongifolius.*"

It is a species of limited distribution, being found on limestone hills and cliffs from central Illinois, across Missouri, to adjacent parts of Kansas, Oklahoma, and Arkansas.

Specimens examined:

(The following abbreviations indicate the herbaria in which the specimens occur: FM = Field Museum; GH = Gray Herbarium; MBG = Missouri Botanical Garden).

ILLINOIS: Carlinville, Sept. 11, 1889, *Andrews* (MBG); same locality, Sept. 4, 1890, *Andrews 1* (GH); Athens, Sept. 1868, *Hall* (FM); Peoria, Sept. 1891, *McDonald* (FM); same locality, Sept. 1890, *McDonald* (MBG); Schuyler Co., Sept. 13, 1872, *Mead 4* (FM); Falling Spring, Sept. 1844, *Engelmann* (MBG); Prairie du Pont, Sept. 1842, *Engelmann* (MBG).

MISSOURI: Allenton, Oct. 10, 1890, *Letterman* (MBG); Hannibal, Sept. 16, 1911, *Davis 1050* (MBG); Clarksville, Sept. 24, 1911, *Davis 1120* (MBG); Branson, Oct. 20, 1907, *Palmer T4* (MBG); Kimmswick, Sept. 27, 1885, *Wislizenus 172* (MBG); Monteer, Oct. 10, 1907, *Bush 4889* (MBG); Swan, Sept. 24, 1905, *Bush 3417* (MBG); Eagle Rock, Sept. 23, 1896, *Bush 297* (MBG); Belleville, Sept. 22, 1908, *Palmer 1339* (MBG); La Grange, Sept. 6, 1915, *Davis 6248* (MBG); Jasper, Oct. 7, 1908, *Palmer 1334* (MBG); Joplin, Oct. 30, 1908, *Palmer 1416* (MBG); Reddings Mill, Sept. 26, 1906, *Bush 5194* (MBG); Fenton, Oct. 9, 1921, *Drushel 4590* (MBG); Jerome, Sept. 25, 1912, *Kellogg* (MBG); Van Buren, Oct. 11, 1920, *Palmer 19471* (MBG); Williamsville, Oct. 20, 1907, *Bush 1107* (MBG); Ironton, Oct. 13, 1920, *Palmer 19531* (MBG); Carl Jct., Oct. 7, 1908, *Palmer 1338* (MBG); Club House, Sept. 11, 1897, *Trelease 702* (MBG);

Oregon Co., Aug. 14, 1893, *Bush* (MBG); McDonald Co., Sept. 1, 1893, *Bush* (MBG); Pond, Oct. 6, 1918, *Aiken* (MBG); Galena, Oct. 11, 1913, *Palmer 4628* (MBG); Pilot Knob, Nov. 1845, *Engelmann* (MBG); Kimmswick, Oct. 11, 1863, *Engelmann* (MBG); Meramec Highlands, Sept. 1843, *Engelmann* (MBG); Dr. Engelmann's garden, Oct. 15, 1872, *Engelmann* (MBG); Seligman, Oct. 24, 1925, *Palmer 29374* (MBG); Greene Co., Sept. 4, 1893, *Bush 142-A* (FM).

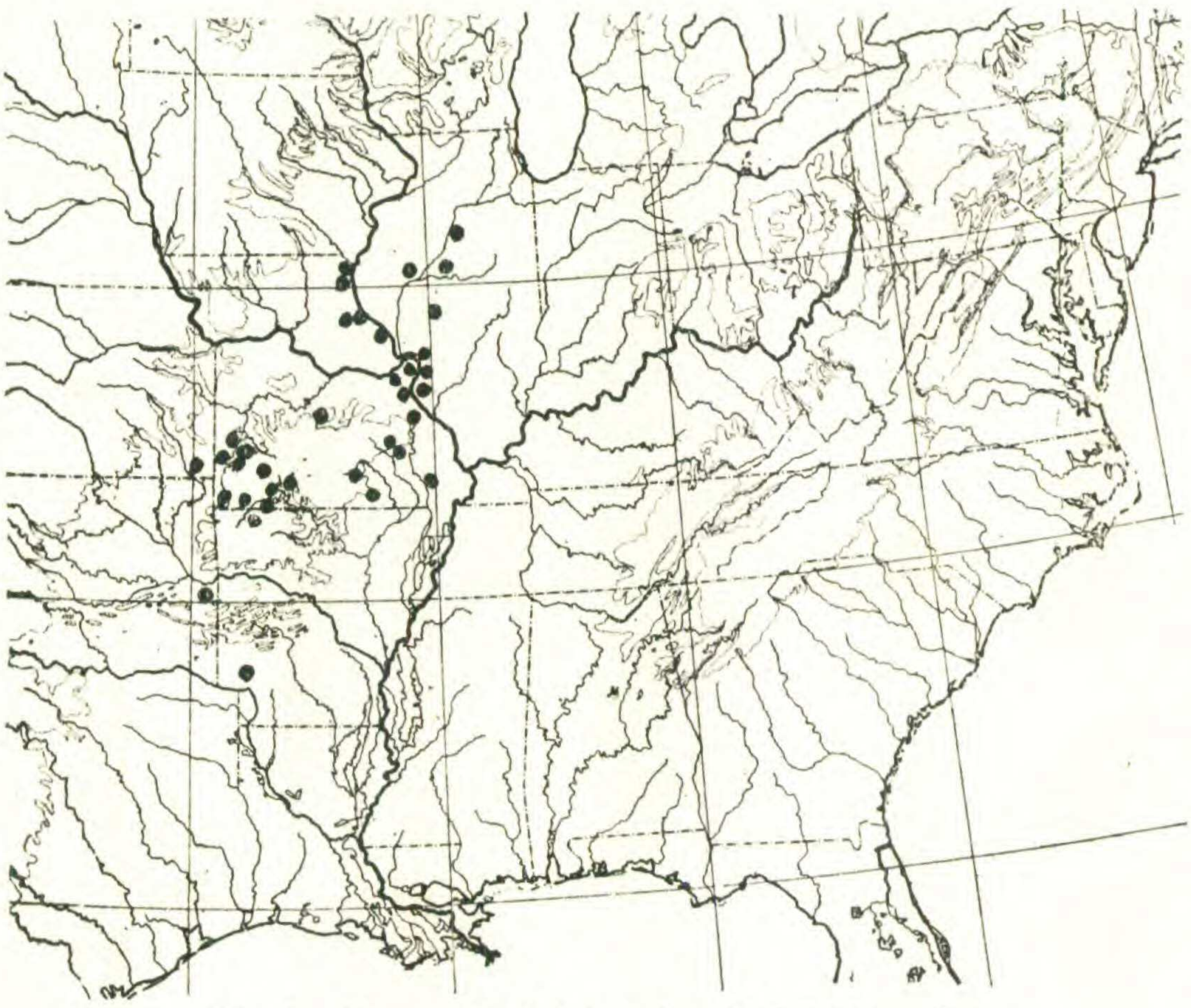


Fig. 1. Geographical distribution of *Aster anomalus*.

Arkansas: McNab, Oct. 19, 1915, *Palmer 8969* (MBG); same locality, Oct. 5, 1923, *Greenman 4440* (MBG); Eureka Springs, Sept. 19, 1913, *Palmer 4367* (MBG).

Kansas: Baxter Springs, Oct. 5, 1925, *Palmer 29029* (MBG).

Oklahoma: Poteau, Oct. 28, 1915, *Palmer 9055* (MBG).

The distribution of the species as shown by the above specimens is illustrated in fig. 1.

III. Variation

In general it may be said that while *Aster anomalus* is extremely variable, the variation centers about what Sinskaya ('28) calls, "a nucleus of common features." Among all the plants examined, including herbarium specimens, plants studied in the field, and over 200 seedlings grown in the experimental plot, there was not a single individual whose specific identity was questionable. All of them were unmistakably *Aster anomalus*. The variation extended to all parts of the plant; leaf number, size, and shape; flower-head number, size, shape, and arrangement; ray number, size, shape, and color; etc. Three characters were studied in some detail: the lower cauline leaves, the flower-heads, and the ripened achenes.

Fig. 2. Outlines of *Aster anomalus*, *A. azureus*, and *A. Shortii* (reading from left to right).

The cauline leaves.—The lower cauline leaves of *Aster anomalus* are very similar to those of the closely related species, *A. Shortii* and *A. azureus*. The leaves of all three species are firm in texture and are ovate or ovate-lanceolate with a cordate base. While they agree on these major points they differ on many minor ones, and *Aster anomalus* can be successfully separated from its closest relatives (or from all the other species of the genus for that matter) by leaf characters alone. Figures 2 and 3 show the main differences between the leaves of the three species. In fig. 2 are typical silhouettes reconstructed from tracings of herbarium specimens. It may be seen that *A. azureus* differs

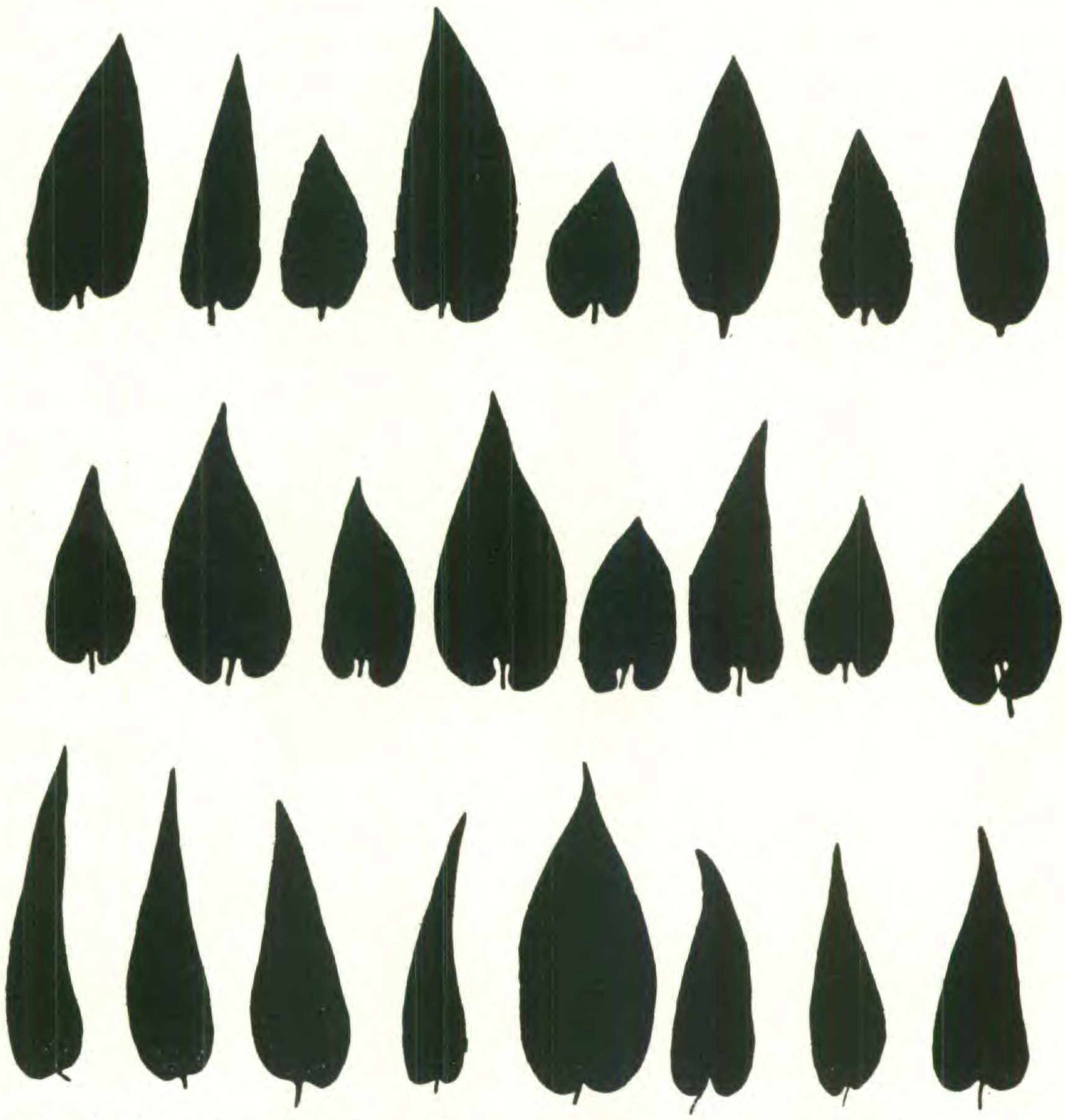


Fig. 3. Variation in outline of lower cauline leaves: upper row, *Aster azureus;* middle row, *A. anomalus;* lower row, *A. Shortii.*

from the other two species in having fewer leaves with only the lowermost cordate at the base and proportionately longer petioles. These differences hold generally for the three species in question.

In fig. 3 are shown tracings of leaf blades from eight specimens of each species. These figures demonstrate that the leaves of *A. anomalus* are more deeply cordate at the base than those of either of the other species. They are also, on the average, less pronouncedly lanceolate than those of *A. Shortii.* From *A. azureus*, in addition to the differences reported above, they are further differentiated by more deeply cordate bases and an almost entire lack of serrations. All of these differences are summarized in table I.

TABLE I

COMPARISON OF CAULINE LEAVES IN THREE SPECIES OF ASTER

A. azureus	*A. anomalus*	*A. Shortii*
Cordate bases on only the lowermost caulines	Cordate bases on most of the large caulines	Cordate bases on most of the large caulines
Petioles proportionately long	Petioles proportionately short	Petioles intermediate
Leaves ovate to ovate-lanceolate	Leaves ovate to ovate-lanceolate	Leaves ovate-lanceolate
Leaf bases cordate or subcordate	Leaf bases deeply cordate	Leaf bases cordate or subcordate
Leaves often serrate	Leaves entire or at most subserrate	Leaves entire or at most subserrate

Flower-heads.—In *Aster anomalus* all the flower-heads of a single individual are usually very similar. Numbers b, c, f, of fig. 4, pl. 4, show three heads from the same plant. It will be noticed that they agree in having numerous rays, which are relatively short, blunt, and regular in outline. On the other hand, the differences between flower-heads on separate plants are very conspicuous. Among the characters which differentiate individuals are: length of rays, number of rays, shape of rays (cleft or not cleft, broad or narrow, straight or waved, etc.),

TABLE II

NUMBER OF RAYS ON INDIVIDUALS OF TWO WILD POPULATIONS COMPARED WITH THAT OF EXPERIMENTAL POPULATION, SBCZG. SBCZG WAS COMPOSED OF SIXTEEN SISTER PLANTS GROWN FROM SEED COLLECTED FROM A SINGLE INDIVIDUAL AT HIGH RIDGE, MO.

	Number of rays													
	19	20	21	22	23	24	25	26	27	28	29	30	31	32
High Ridge, Mo.			1				1	2			1	1		1
Rankin, Mo.		1	1		1					1			2	1
Sbczg	1	2		2	1	1	2	3	1		1	2		

TABLE III

LENGTH OF RAY (LIGULE) IN MM. FOR THE SAME INDIVIDUALS REPORTED IN TABLE III

	Length of ray										
	6	7	8	9	10	11	12	13	14	15	16
High Ridge, Mo.			1		2	1		2	1		
Rankin, Mo.		1				1	1	1	2		1
Sbczg		1	2	2	3	4		3	1		

width of disk, number of disk-flowers, etc. Exact determinations of ray number and ray length were made for two small populations and are summarized in tables II and III. The correlation

TABLE IV

CORRELATION BETWEEN NUMBER OF RAYS AND LENGTH OF RAY

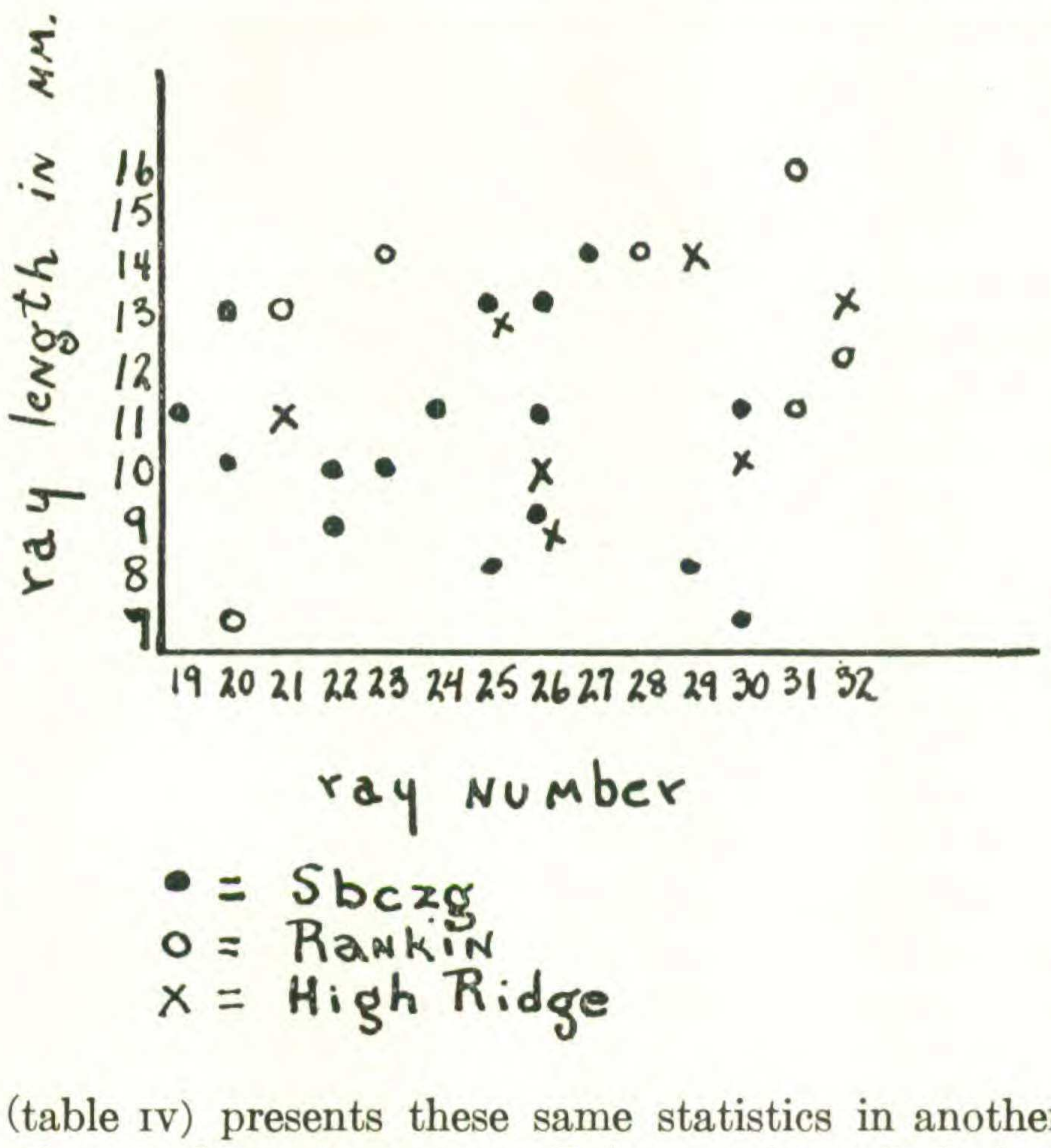


table (table IV) presents these same statistics in another way. While the numbers are too small for precise calculation, it is apparent from mere inspection of the table that there is no very evident association between length of rays and number of rays

(i. e., plants with long rays do not tend to have more rays than plants with short ones, and *vice versa*).

Achenes.—The ripened achenes of *A. anomalus* were found to be highly diagnostic. Specimens from three widely separated localities are illustrated in pl. 4, fig. 2, compared with single specimens of *A. azureus* and *A. turbinellus.* The plate shows how constant are the dark color, the prominent ribs, and the other peculiarities which characterize *A. anomalus.* Achenes from ten to fifteen other species of the genus *Aster* were acquired from herbarium specimens and wild plants. Those of *A. anomalus* were clearly differentiated from all of those examined.

With the achene, therefore, as with the leaf, careful examination revealed characters which would permit of specific determination by that one feature alone.

It was unfortunately not possible to obtain ripened achenes of *A. Shortii.* Immature specimens indicated that they are probably more like *A. anomalus* than any of the other species studied. Seed characters are useful because of their relatively imperishable nature. It is therefore all the more unfortunate that collectors have so entirely neglected fruiting material of the genus *Aster.* The herbarium of the Missouri Botanical Garden is particularly rich in specimens of *A. anomalus,* possessing well over a hundred sheets, only five of which exhibit well-ripened achenes. Collectors should realize that though fruiting material of *Aster* may not make neat-looking specimens, it is nevertheless extremely useful in taxonomic work.

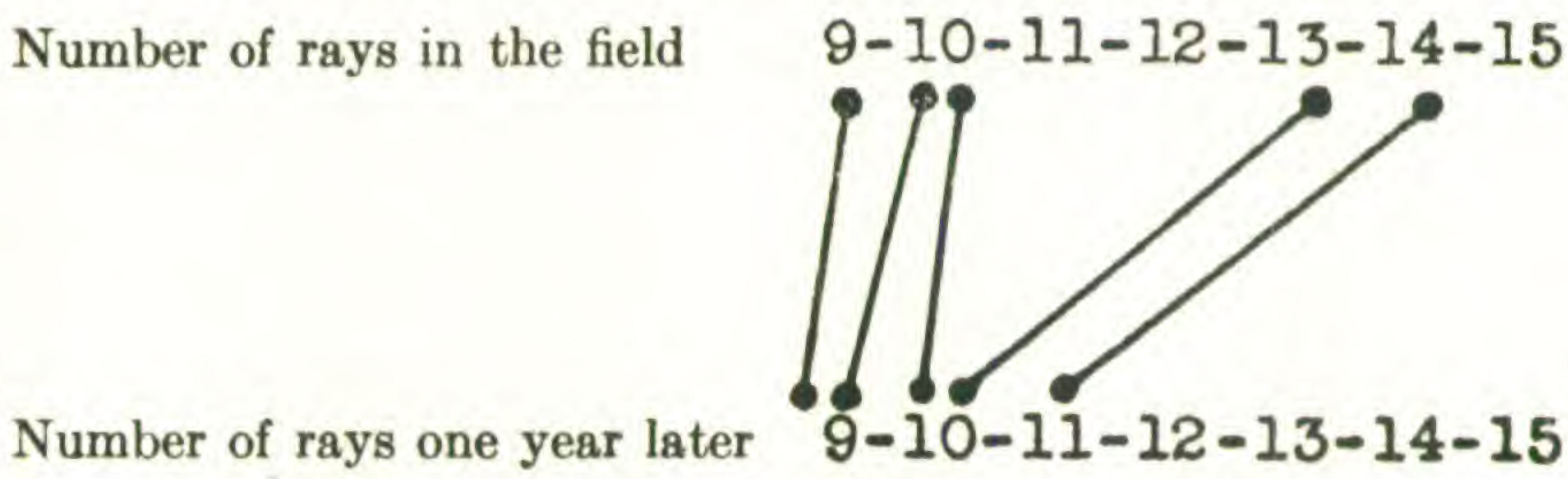
IV. Experimental

Representative individuals from several localities were transplanted to the experimental plot at the Missouri Botanical Garden. Superficially the species was greatly changed by cultivation. The stems were taller, they branched more freely, and the number of flower heads was greatly increased. Plate 4, fig. 5, shows one of the smallest garden-grown plants, and figs. 1 and 3, branches from other individuals. On the other hand, closer examination showed that most individual characteristics persisted, in spite of the changes produced by cultivation. The shape and relative size of the disks and rays remained the same.

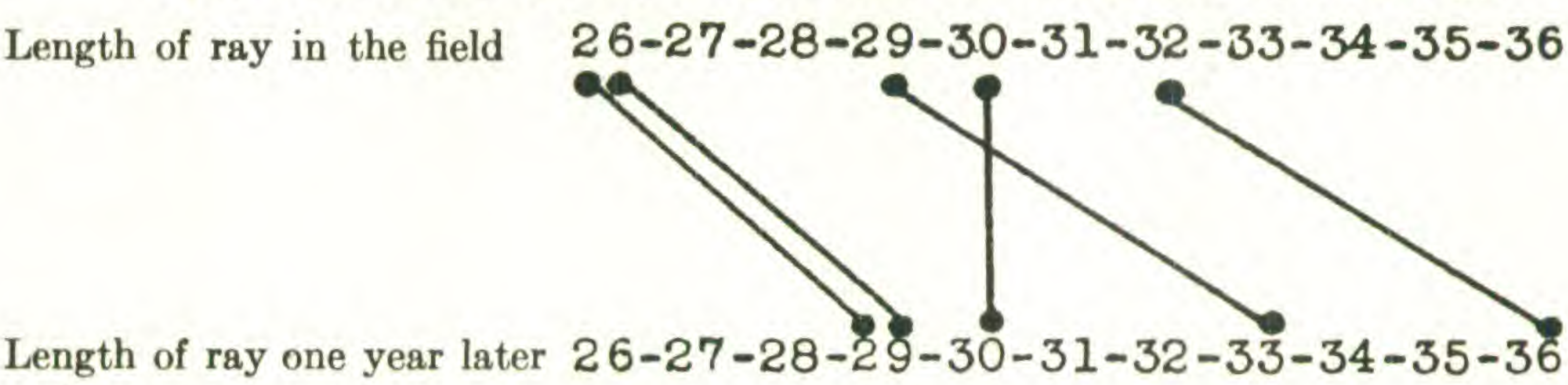
Plants with deeply notched ligules collected at High Ridge, and Rankin, Mo., continued to bear flowers with similarly notched ligules for year after year in the experimental garden. Table v gives exact data on ray number and length for five individuals before and after transplanting. It shows that while the absolute numbers have been somewhat changed, the comparative relations between individuals have remained practically the same.

TABLE V

NUMBER OF RAYS IN FIVE INDIVIDUALS BEFORE AND AFTER TRANSPLANTING—AVERAGES OF FIVE HEADS EACH



LENGTH OF RAY IN MILLIMETERS FOR FIVE INDIVIDUALS BEFORE AND AFTER TRANSPLANTING—AVERAGES OF FIVE HEADS EACH



From these experiments it was concluded that aside from general habit, the differences which exist between individuals in the wild have a strong germinal basis. A further series of experiments was made to determine the genetic relationships between these individual differences. Seeds were collected from five plants growing under natural conditions, three at High Ridge, Mo., and two at Rankin, Mo. The seeds were sown in separate lots and grown as five series of sister (or to be more exact, half-sister) seedlings. Within each group no two plants were alike or even similar; in fact there was almost as great a range of variation in each group of sister seedlings from one mother plant as there was in all the wild plants examined at either High Ridge or Rankin.

Some of the most conspicuous differences between the sixteen sister seedlings of group Sbczg are tabulated in table VI. The data for number and length of rays are included in tables II and III referred to above. The variation between sister plants is illustrated in pl. 4, fig. 4, where three flower heads from one individual (b, c, f) are contrasted with one each from three sister plants.

TABLE VI

COMPARISON OF SISTER SEEDLINGS, GROWN FROM SEED COLLECTED FROM A SINGLE PLANT

	Ray color	Ray length	Ray number	Ray form	Inflorescence type
Sbczg— 2	Medium	11	30	Irregular	Loose
Sbczg— 3	Medium	10	20	Irregular	Loose
Sbczg— 4	Medium	13	26	Irregular	Very loose
Sbczg— 5	Dark	13	25	Medium	Loose
Sbczg— 6	Medium	14	27	Irregular	Very loose
Sbczg— 7	Light	7	30	Irregular	Compact
Sbczg— 8	Medium	11	26	Irregular	Medium
Sbczg—10	Medium	10	23	Irregular	Loose
Sbczg—11	Light	11	19	Irregular	Compact
Sbczg—12	Light	10	22	Narrow	Medium
Sbczg—13	Medium	9	22	Irregular	Medium
Sbczg—14	Light	11	24	Irregular	Medium
Sbczg—15	Medium	8	29	Medium	Loose
Sbczg—16	Medium	8	25	Irregular	Loose
Sbczg—17	Light	9	26	Irregular	Loose
Sbczg—18	Light	13	20	Irregular	Medium

In the other four groups the morphological relations between sister seedlings were substantially the same. It was therefore concluded that *Aster anomalus* is a highly heterozygous species. In nature it is so often outcrossed that there is no opportunity (as in a self-pollinated species) for the establishment of more or less true-breeding strains within the species. Rather do the differences which characterize individuals combine and recombine anew in every generation, interweaving in precisely the same fashion as do individual characteristics in human families.

V. Summary and Conclusions

1. *Aster anomalus* is a well-differentiated species ranging from central Illinois, through Missouri to adjacent parts of Kansas, Oklahoma and Arkansas.

2. Individual variation, though extremely conspicuous, centers around a "nucleus of common features." Among all the speci-

mens examined and the seedlings grown, there was not one which did not clearly belong to *A. anomalus*.

3. Intensive study of the leaf and the achene revealed characteristics which would make specific identification possible by either feature alone.

4. Transplanting experiments demonstrated that the size and general habit of the individual are largely influenced by the environment. Ray-floret and disk-floret characters, on the other hand, have a strong germinal basis and remain practically unchanged by cultivation.

5. Progeny tests were made of five wild plants from two localities in Missouri. In each of the resulting families of sister seedlings there was a high degree of variation; almost as much as had been found among all the wild plants at either of the localities where seeds were collected. It is concluded that *A. anomalus* is a highly heterozygous species.

Four points related to the problem of species are discussed in the light of these results:

I. Species of the genus *Aster* are notoriously difficult to classify. Dr. Gray, the foremost student of the group, found them very puzzling. We find in his letters (Gray, '93) many references like the following: "I am half dead with Aster. I got on very fairly until I got into the thick of the genus, among what I called Dumosi and Salicifolia. Here I work and work, but make no headway at all. I can't tell what are species and how to define any of them * * * I never was so boggled * * * If you hear of my breaking down utterly, and being sent to an asylum, you may lay it to Aster, which is a slow and fatal poison,"

Wiegand, in his recent report on *Aster lateriflorus* ('28), echoes the same sentiments. It is therefore a point of some theoretic interest that *A. anomalus* should be such an absolutely clear-cut and unmistakable species. It shows that the uncertain speciation found in *Aster* and certain other genera is not necessarily characteristic of the whole genus, but that among a maze of intergrading species there may be some which are well-defined. Or to put it in others words: "Bad" species may have close relatives which are "good" species. This point has a bearing on certain evolutionary theories. At various times and in various ways, the suggestion has been made that whole groups of species may go through "mutating periods," and the genus Aster has sometimes been advanced as one whose species are in a nascent condition. The facts reported above show that here is one species of *Aster* which, though showing unmistakable affinities to other species of the genus, is itself clear-cut and well-defined.

II. Modern genetic research would have us suppose that the differences between species are located in the chromosomes and the other elements of the cell. If this hypothesis is true we would expect to find specific differences expressed throughout the entire organism. The work reported above shows that such is indeed the case in *A. anomalus.* Critical study revealed characteristics which would permit of identification by the leaves or achenes alone. Similar characters could probably have been found for the involucral bracts and for the disk and ray florets. Viewed in the light of these results disputes as to how many characters are necessary for specific delimitation seem rather trivial. Given abundant material it should be possible to find—and even more, to demonstrate—specific differences in all those parts of the plant where germinal differences are not swamped by environmental ones.

III. The fact that a cross-pollinated, continuously outbred species, such as *Aster anomalus,* can still as a whole remain a clear-cut morphological unit, offers serious difficulties to the universal application of the Jordanon, as the writer has already pointed out ('28). The germinal differences between individuals of *A. anomalus* are so many that the chances of finding any two plants which are even phenotypically similar are practically *nil.* If the Jordanon terminology were to be consistently applied it would be necessary to give a name to every individual examined. Clearly in this case, the only practical morphological unit is the whole complex of interweaving individualities which makes up the Linnaean species. Nor is the condition reported here in any sense exceptional. Babcock and Hall ('24), have reported similar conditions for the inheritance of individual differences in *Hemizonia congesta,* and it would be expected that any cross-pollinated species would behave likewise. Since cross-pollination is more common than self-pollination, the existence of recognizable Jordanons within Linnaean species would seem to be the exception and not the rule.

IV. It is the writer's provisional opinion ('28) that without a high degree of isolation, individual differences are not effective in species forming (among the higher plants at least). The facts reported in this paper lend further support to that hypothesis. *Aster anomalus* would seem to be a species which remains a consistent and independent unit in spite of a high degree of variation between individuals.

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EXPLANATION OF PLATE

PLATE 4

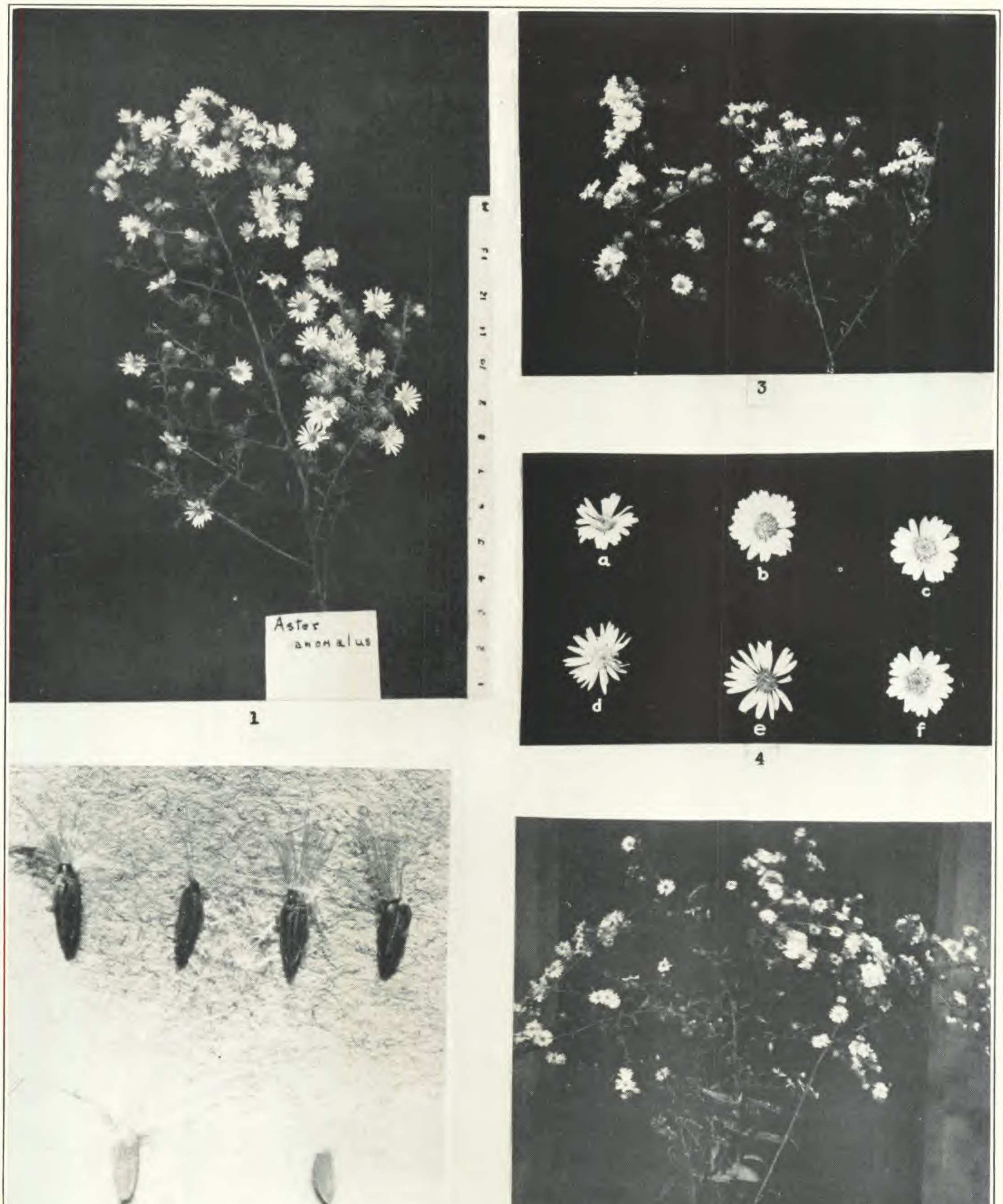
Fig. 1. Flowering branch of garden-grown specimen of *Aster anomalus;* 14-inch rule for comparison.

Fig. 2. Ripened achenes, × 3½. Upper row, *Aster anomalus* from the following four localities, reading from left to right: Rankin, Mo., Van Buren, Mo., St. Louis, Mo., Poteau, Okl.; lower row, *Aster turbinellus* and *Aster azureus.*

Fig. 3. Flowering branches from two garden-grown plants of *Aster anomalus.*

Fig. 4. Flower heads of *Aster anomalus,* × ½: *b, c, f,* three heads from the same plants; *a, d, e,* heads from three other plants.

Fig. 5. Garden-grown plant of *Aster anomalus.*



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